Vol. VII. *July, 1904.* *No. 2*

BIOLOGICAL BULLETIN

THE MORPHOLOGY OF THE MADREPORARIA. V. SEPTAL SEQUENCE.[1]

J. E. DUERDEN.

The skeleton of an ordinary polycyclic hexameral coral presents a series of septal partitions arranged in a radiating manner, and in any cycle the constituent septa are equal in size and alternate in a regular manner with the members of the other cycles. In general, the cyclic plan of a corallite is 6, 6, 12, 24, 48, etc., and the number of septa in any cycle beyond the first corresponds with the total number in all the cycles within. As the septa in any cycle are alike in size it seems reasonable to suppose that they all appeared simultaneously in the growth of a coral, a cycle at a time, and also that the inner larger cycles were developed before the outer smaller cycles; in other words, the relative sizes and positions of the septa in the mature corallite would seem to represent their order of development.

Much attention has already been given to the subject of the order of appearance of the septa in corals by different writers. The rule which Milne-Edwards and Haime give in their "Histoire Naturelle des Coralliaires" (1857) is well known, appearing in all text-books describing recent or fossil corals. The authors assume that in the case of the first three cycles the constituent septa of each cycle appear simultaneously, a cycle at a time, and that the relative development of each cycle corresponds with its relative size or distance from the center of the calice. From the fourth cycle outwards, however, a different sequence is

[1] The first two parts of this series of papers appeared in the *Johns Hopkins University Circulars*, Vol. XXI., Nos. 155 and 157, and were reprinted in the *Annals and Magazine of Natural History*, Ser. 7, Vol. X., May and August, 1902. The third and fourth parts appeared in the *Annals and Magazine of Natural History*, Vol. X., November, 1902, and Vol. XI., February, 1903. The work is being carried out with the assistance of an appropriation from the Carnegie Institution.

Contributions from the Zoölogical Laboratory of the University of Michigan. No. 81.

assumed for the various members of a cycle, according to their relation to the members of the inner cycles.

Professor A. Schneider in 1871 and Professor C. Semper in 1872 also discussed the same subject. The former agrees with Milne-Edwards and Haime as regards the manner of development of the first three cycles: first a cycle of six appears, then a smaller cycle of other six alternating with the first, and later a cycle of twelve septa which are smaller and alternate with the twelve making up the first and second cycles. In the further growth Schneider considers that the septa of a newer cycle may so enlarge in size as to appear to belong to an older cycle, and thus the primary sequence and hexamerism become lost.

Semper holds that no constant rule for septal development can be established, that the manner of growth varies more or less with each species.

Professor G. von Koch, in the course of his prolonged studies on the morphology of corals, has also made certain observations upon the laws of septal development, particularly in his paper "Das Vermehrungsgesetz der Septen," 1881. His results are based mainly upon serial sections of individual coralla of *Caryophyllia*, and lead him to conclude (p. 93) in the main in favor of the validity of the sequence given by Milne-Edwards and by Schneider: "Bei den sechszahligen Korallen, sowohl den Eporosen als den Perforaten, wachst die Zahl der Sternleisten (Septa) in der Art, dass sich nahezu gleichzeitig im ganzen Umfang des Kelches zwischen je zwei alteren eine jungere anlegt, also die Zahl der Sternleisten eines folgenden Cyclus immer gleich ist der Summe aller vorher vorhandenen. Alle Ausnahmen von dieser Regel sind auf direxte Anpassungen oder erblich gewordene Veranderungen im Wachsthum des ganzen Thieres zuruckzufuhren."

All the above conclusions are based mainly upon the examination of adult coralla, in which there is available for comparison only the relative sizes of the septa and their order of appearancein serial sections. The actual details of growth of the septa indeveloping corals, in their relationships to the mesenteries, have in no instance been followed beyond the first two cycles. Professor H. de Lacaze-Duthiers (1873, '94, '97) and Professor G. von Koch (1882, '97) have both studied the early development of the skeleton in

corals, but their results throw no certain light upon the difficult problem of the manner of increase of the septa beyond the two primary cycles, nor of the relation of these to the later cycles.

Observations which I have been able to make upon the growth of the septa in larval polyps of the common West Indian coral, *Siderastrea radians* (Pallas), show the unreliability of assuming the developmental sequence from adult relationship, and give an interpretation to the later septal sequence altogether different from any hitherto proposed.

Larvæ of *Siderastrea*, fixed to fragments of glass, and capable of being examined as transparent microscopic objects, were followed in the course of their development as young polyps for a period of four months, and the order of appearance of their septa determined as far as the completion of the first three cycles.

In every case it was found that the six members composing the first cycle appeared simultaneously. This takes place shortly after the larva settles, at a stage when the young polyp has six pairs of mesenteries, arranged as in Fig. 1, where all the mesenteries are complete except the fifth and sixth developmental pairs. The septa are alike in size and situated at equal distances apart within the entocœles of the six primary pairs of mesenteries. Later development proves, as would be expected, that the six primary septa of the mature corallite are the direct enlarged representatives of the six septa first to appear in the larval polyp.

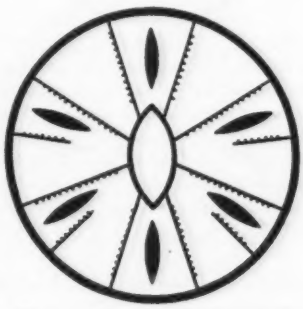

FIG. 1. Diagrammatic arrangement of the mesenteries and septa on the appearance of the first cycle of six septa. The septa are situated within the six primary entocœles, and the six alternating mesenterial chambers, devoid of septa, are the primary exocœles. The directives are situated at the opposite extremities; the two bilateral pairs of incomplete mesenteries are the fifth and sixth pairs in the mesenterial sequence. The upper border is regarded as dorsal and the lower as ventral.

As regards the primary cycle in *Siderastrea* the surmise that adult size corresponds with developmental sequence is therefore correct. Moreover, in the early

stages of septal growth secured by Lacaze-Duthiers in *Astroides*, *Flabellum*, *Balanophyllia*, *Caryophyllia*, etc., and also by von Koch in *Astroides* and *Caryophyllia*, the six primary septa appeared simultaneously, and were equal from the beginning.

In *Siderastrea* the second cycle of six septa began to appear a few days after the primary cycle, its members situated within the exocœlic chambers, thus alternating with the six entosepta (Fig. 2). In a few polyps the septa appeared simultaneously and were all practically equal, but in most individuals a marked difference was manifest; the dorsal and middle pairs of exosepta arose bilaterally in advance of the two ventral pairs, and for a time the dorsal pairs were a little larger than the middle. Within a short time the two ventral exosepta appeared, but remained smaller than the others. Thus at this early stage a decided dorso-ventrality in the development of the septa was apparent, which gave a bilateral character to the polyp as a whole (Fig. 2).

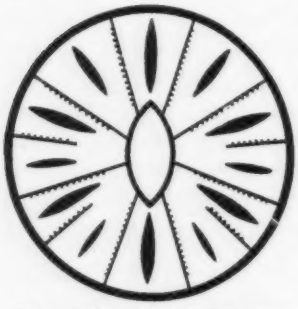

FIG. 2. Arrangement of the mesenteries and septa after the establishment of the first and second septal cycles—six entosepta and six exosepta. The dorsal pair of exosepta are somewhat larger than the middle pair, and the middle pair are larger than the ventral pair, thus giving a bilateral character to the corallum.

In most of the developing corals investigated by Lacaze-Duthiers and von Koch the entocœlic and exocœlic cycles either appeared together, or one shortly after the other, as in *Siderastrea*. In most cases it was found that the members of either cycle arose simultaneously, in a truly radiate manner, without passing through a bilateral stage, though Lacaze-Duthiers figures a very decided bilateral condition in the early development of the skeleton in *Astroides* (1873, Pl. XIII., Fig. 29).

The next stage in the growth of the septa in *Siderastrea* is well defined, but is not so clear as to its significance. After the condition shown in Fig. 2 was reached the septa began to enlarge at their peripheral extremity; in some instances the enlargement

took place by the direct extension of the septa already developed, and in others by the deposition of separate skeletal nodules. The new growth was arranged in a V-shaped manner, the angle of the V being larger in the exosepta than in the entosepta (Fig. 3). In the diagrammatic figure the additions are all represented as separate calcareous fragments, but no constancy was apparent in the different septa as to the freedom or fusion of the extensions at this stage. In all the polyps the enlargement of the ventral exosepta was much behind that of the dorsal and middle exosepta, and usually it could be seen that the middle exosepta did not enlarge as rapidly as the dorsal.

At a somewhat later stage, each septum became a continuous structure, owing to the complete fusion of the free nodules in the

FIG. 3. Stage showing the peripheral enlargement of the septa which occurs in a bifurcating manner by the addition of separate nodules. The ventral exosepta grow more slowly than the middle and dorsal pairs.

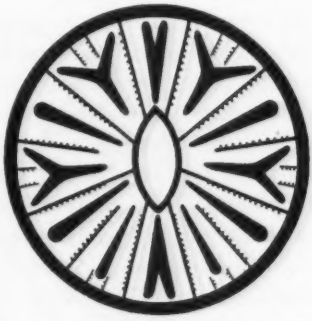

FIG. 4. Further enlargement of the septa by fusion of the nodules, and establishment of the six pairs of second cycle mesenteries; the latter, like the exosepta, decrease in size from the dorsal to the ventral border.

process of growth. The entosepta then appeared as simple formations, much broader peripherally than centrally, though the two directive entosepta showed traces of the earlier bifurcation longer than the four lateral entosepta; the exosepta, on the other hand, remained strongly bifurcated, with the exception of the ventral pair, the members of which enlarged comparatively little (Fig. 4).

A similar bifurcated stage, due to the appearance of independent calcareous nodules, occurs in the development of *Astroides*,

Caryophyllia, and some other corals, but hitherto its significance has not been satisfactorily explained. At one time the separate fragments were supposed to be concerned in the formation of the thecal wall, but it will be seen that such is certainly not their fate in *Siderastrea*.

About this time, the polyps being two months old, the second cycle mesenteries began to appear on the column wall, situated in the exocœlic chambers between the primary mesenteries (Fig. 4). In their development they also presented a conspicuous dorso-ventrality: the two first pairs appeared within the dorsal exocœles, the moieties of each pair arising at the same time and remaining equal; the two next pairs were within the middle exocœles; and finally appeared the pairs within the ventral exocœles. The dorso-ventral succession thus followed by the six pairs remained evident throughout the period under observation, the dorsal pairs being larger than the middle, and the middle larger than the ventral. The comparative development of the first and second cycle mesenteries at this period, and their relationship to the septa, are shown in Fig. 4. A similar bilateral, dorso-ventral succession of the second cycle mesenteries has long been known to occur in the development of actinian polyps, in contrast to the simultaneous origin at one time assumed.

Clearly the next skeletal stage will be one involving the establishment of septa within the entocœles of the second cycle of mesenteries, and these will constitute the second cycle of septa of the adult corallite. Hitherto it has been generally assumed that where a cycle of exosepta is already developed, and then a new cycle of mesenteries appears within the corresponding exocœles, that the exosepta already present become included within the entocœles of the new mesenteries, and thus become entosepta; an additional outer cycle of exosepta appears later and its members in their turn become entosepta. Thus Delage and Hérouard in their "Traité de Zoologie Concrète" (1901, p. 558) remark: "Quand, dans les interloges occupées par les septes du dernier cycle, naît un nouveau cycle de couples de cloisons, celles-ci se forment de part et d'autre du septe interloculaire qui, de ce fait, devient loculaire, et bientôt un nouveau cycle de septes se forme dans les nouvelles interloges qui vien-

nent d'être formées. Les cycles naissent successivement et jamais un cycle ne commence à se former avant que le précédent soit complete." Similarly J. Stanley Gardiner (1902, p. 133) in his account of the anatomy of *Flabellum rubrum* says (italics added): "As the growth of any corallite proceeds, more and more septa up to six cycles appear. *The former exocœlic order of septa becomes entocœlic by the development of new pairs of mesenteries.* The increase of mesenteries takes place *pari passu* with the formation of new septa."

Unfortunately, the relationships involved in the above assertions have not been actually followed, though from the known conditions no other arrangement at first sight seems possible; and it was principally with a view to determine the truth or otherwise of the assumption that the present investigation was undertaken.

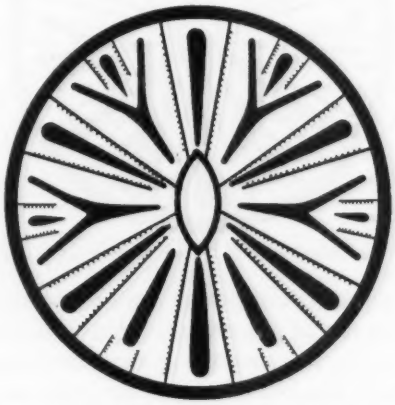

FIG. 5. First appearance of the permanent second cycle of entosepta situated within the entocœles of the second cycle of mesenteries and the bifurcations of the dorsal and middle exosepta.

Shortly after the stage represented in Fig. 4 was reached independent calcareous growths began to arise peripherally, in positions corresponding with the entocœles of the second cycle mesenteries; those within the dorsal entocœles were larger than the ones within the middle entocœles, while for a long period there was no corresponding formation within the ventral entocœle (Fig. 5). At first the structures were quite free and resembled

small independent septa ; they suggest a new series of entocœlic septa, appearing in a dorso-ventral sequence like the mesenteries with which they are associated.

Later these new septa extended more centrally, and necessarily came into union with the simple inner portions of the septa which originally constituted the exocœlic second cycle. Several of the polyps were reared until the new second and third orders of septa were fully established, when they presented the arrangement shown in Fig. 6. The peripheral, primarily independent septa

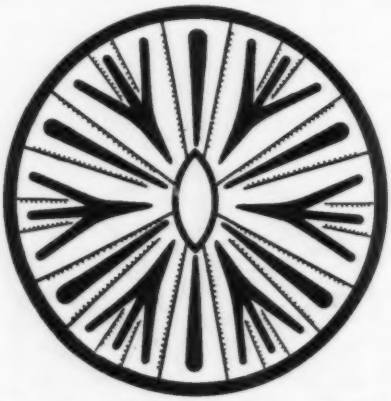

FIG. 6. Completion of the first three cycles of septa.

within the second cycle entocœles have all become continuous with the median part of the original second cycle exosepta, and along with them now constitute the permanent second cycle of entosepta ; while the bifurcations of the exosepta now constitute the third cycle of twelve septa and are seen to be exosepta.[1] It will also be seen that the growth within the ventral system has now attained the same stage as that within the middle and dorsal systems, so that the corallite as a whole presents nearly perfect radial symmetry.

The stages thus passed through are of great importance in their bearing upon several obscure points in coral development and morphology, and call for fuller consideration. In the first

[1] In the adult corallite of *Siderastrea radians* the exosepta are fused by their inner ends with the entosepta as represented in Fig. 6 and Fig. 7*g*.

place, it is seen that the second cycle entosepta, which are to become the permanent second cycle of the adult corallite, arise as independent formations, though later they fuse with the septa which constituted the original second cycle, the two series being situated along the same radii. They are to be regarded as altogether new formations which replace the original second cycle exosepta; the fact that they fuse with the latter in their forward growth would seem to be of incidental importance, depending upon the fact that they are in the same radii. Secondly, the original second cycle exosepta of Fig. 2 lose their morphological individuality, becoming involved in the new second cycle entosepta as the latter continue their growth centrally; they are merely the temporary predecessors of a later permanent cycle.[1] As primary second cycle exosepta they do not become included within the entocœles of the second cycle mesenteries, but only as the central continuations of the new second cycle entosepta.

The results thus afford definite proof that the exosepta of a former stage do not become the entosepta of a later stage when another series of mesenteries has appeared with the entocœles of which they correspond. It is manifest that such a conclusion could only be established in *Siderastrea* by actual observation of all the intermediate stages. When the condition represented in Fig. 6 has been reached there is no means of determining the actual two-fold origin of the second cycle entosepta. It is such conditions which have hitherto been studied, and from these no other explanation than that given by Delage and Hérouard and by Gardiner on page 70 would have been expected. Entosepta throughout would now appear to be new formations, not the continuations of the exosepta of a previous stage, and further, they arise after the mesenteries within the entocœles of which they are situated.

[1] In many corals the original second cycle exosepta appear to continue their independent growth *in situ* without losing their identity in the central extension of the entosepta. I believe it will be found that this is the true nature of *pali*, which are found in some corals as small septum-like plates in front of the larger septa. The fact that pali seem not to occur before the primary cycle of six septa, but only before those of later origin, is what we should expect if this surmise be correct. The primary entosepta have never had exocœlic predecessors, as is the case with the later entosepta. Pali would thus represent the persistent exocœlic predecessors of the entosepta beyond the primary cycle which have not lost their individuality in the later growth of the entosepta.

The significance of the twelve exosepta which constitute the outermost third cycle remains to be considered. They undoubtedly represent the direct continuations of the bifurcations of the six primary second cycle exosepta, but their relationships have now changed; instead of appearing as extensions of an older cycle of septa they themselves constitute a cycle. The details exhibited by the particular species studied seem inconclusive towards determining whether the exosepta of the later stage are to be regarded as but continuations of the exosepta of the previous stage or as entirely new formations. The former would certainly seem to be suggested; probably the point could be definitely established in some other coral species in which the exosepta in the adult are not fused at their inner extremity with the entosepta. Whichever view is accepted the exosepta of the third cycle are obviously developed in advance of the entosepta of the second cycle.[1] Thus the relative sizes and positions which the cycles will ultimately assume in the mature calice do not represent their actual order of appearance.

A third important morphological relationship is definitely established, namely, that the later septa do not arise a cycle at a time as is usually assumed, any more than do the mesenteries. Beyond the primary cycle of six entosepta, the members of which always appear simultaneously, there is a decided dorso-ventrality in the sequence of the septa of each cycle, which for the time being gives a marked bilateral symmetry to the corallum. It is only later, when the development of the septa within each sextant has reached the same stage, that an approximate equality and radial symmetry is attained. Thus the primary symmetry in corals is bilateral, and the arrangement is retained for a long period in the ontogeny of both mesenteries and septa. Therefore in the individual septa making up a cycle, as has been proved for the cycle itself, the adult size does not represent the actual order of appearance.

To return to the further development of the septa in *Sideras-*

[1] It is worthy of note in this connection that the exotentacles in *Siderastrea radians* have been found to appear thoughout in advance of the entotentacles, being the only zoantharian in which this relationship is known to occur. Hence there is nothing contrary to the laws of hexactinian development in the above conception that the exosepta beyond the first series appear in advance of the corresponding entosepta.

trea. The larval polyps were not reared beyond the completion of the first two cycles of mesenteries and the first three cycles of septa (two cycles of entosepta and one of exosepta). On any colony, however, are many developing polyps which present intermediate stages between the commencement and completion of the third cycle of mesenteries and the fourth cycle of septa; and from these results have been obtained supplementary to those already presented. Mature polyps of *S. radians* have rarely more than three cycles of mesenteries and four cycles of septa (three inner cycles of entosepta and an outermost cycle of exosepta).

First, it may be ascertained what are the relationships between the third cycle exosepta of Fig. 6 and the third cycle entosepta and fourth cycle exosepta found in the mature corallite. By means of serial sections through decalcified immature bud polyps it has been possible to establish the relationship of these with respect to one another and to the new mesenteries of the third cycle. The results are diagrammatically represented in Fig. 7 (*a* — *g*), the complications due to the presence of synapticula being omitted. Fig. *a* represents a section through an exoseptum of the third cycle, corresponding to one of the exosepta in Fig. 6, only that the peripheral extremity is now bifurcated. It is in the same stage as each of the four exosepta of the second cycle in Fig. 4, but is shown united with the calicinal wall, and no mesenteries have as yet appeared within the two limbs. Fig. *b* shows the same septum taken from a section at a higher level. Within the exocœlic bifurcation there has now appeared a pair of third cycle mesenteries, in every way comparable in their relationships to the third cycle exosepta with those of the second cycle mesenteries to the second cycle exosepta of Fig. 4.

Fig. *c*, from a still higher level of the polyp, reveals a further stage. Within the entocœle of the mesenteries is seen the rudiment of a third cycle septum. The latter is a new formation, comparable with the rudiments of the second cycle entosepta shown in Fig. 5. One limb of the exoseptum has also become free.

Fig. *d*, taken from a section above that of Fig. *c*, shows the new entoseptum becoming larger, and extending centrally further

than the mesenteries, which in their turn have also increased in size. Both limbs of the bifurcated septum are now free from the middle portion; they represent two independent exosepta becoming distinct from the single exoseptum of a previous cycle (*cf.* Fig. 6) of which they were originally continuations.

Fig. *e* is from a section through the column wall, the septa at this level being exsert, that is, extending above the calicinal wall.

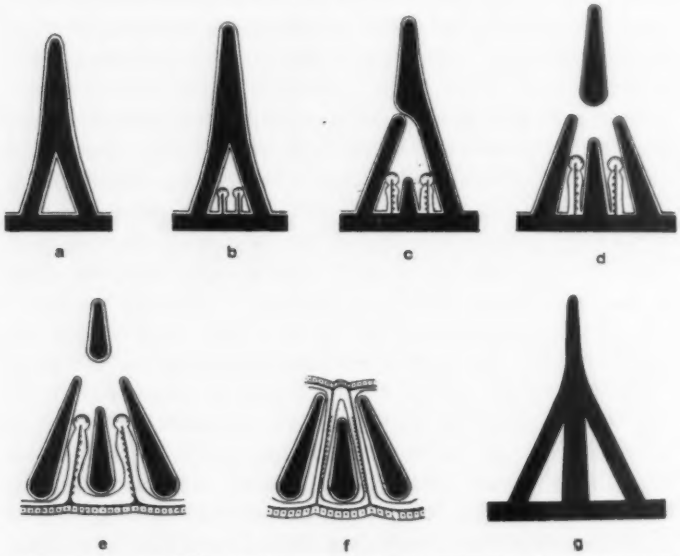

FIG. 7 (*a–g*). Series of diagrammatic figures illustrating the developmental relationships of a pair of third cycle mesenteries and a third cycle entoseptum, in association with a bifurcated third cycle exoseptum.

The relationships shown are the same as in the previous figure, but the inner radial portion of the original third cycle exoseptum has almost disappeared. Fig. *f* is through the column wall (lower) and disc (upper). The mesenteries now extend from one wall to the other, the polyp being in the retracted condition, and the entoseptum is still smaller than the exosepta, one on each side of it. It is manifest that in the later growth the entoseptum will extend more centrally, and come into union with the original third cycle exoseptum which is in the same radius (Fig. *g*), exactly as in the larval polyp shown in Figs. 5 and 6.

The series of sections thus reveals that the third and fourth cycles of septa and the third cycle of mesenteries are related in the same manner as are the second and third cycles of septa and the second cycle of mesenteries; the third cycle entosepta have third cycle exocœlic antecedents. The results may be arranged as follows:

(*a*) The originally simple third cycle exosepta, themselves formed as bifurcations of simple second cycle exosepta, become bifurcated at their peripheral extremity.

(*b*) Within each bifurcation there appears a new pair of third cycle mesenteries, and then within the entocœle of the pair is formed a third cycle entoseptum.

(*c*) The new entoseptum fuses with the central portion of the third cycle exoseptum, while the bifurcations of the latter constitute two new exosepta of the fourth cycle, and are fused at their inner extremity with the entoseptum embraced by them.

Presumably the same process as above outlined will be followed within the two exocœlic chambers of each sextant of the polyp, so that in the end there will be twelve entosepta forming the completed new third cycle and twenty-four exosepta forming the completed new fourth cycle.

The actual sequence according to which the third and fourth cycles of septa are formed remains to be noticed.

The septa alone in the dried corallum are insufficient for this purpose, as they afford no certain means by which the directive axis can be determined, and from this the dorsal and ventral borders of the calice. It has been shown, however, that the mesenteries associated with the entosepta appear in pairs only a little in advance of the entosepta within them; therefore if the sequence of the mesenteries be determined it can be assumed that the septa follow the same order.

From colonies of *Siderastrea* sections of a large number of bud polyps at different stages of development have been prepared, and from these it has been possible to determine the order of appearance of the twelve pairs of third cycle mesenteries. This is indicated in the series of diagrammatic figures in Fig. 8 (*a–d*). In Fig. 8 *a*, in addition to the primary and secondary cycles, a pair of third cycle mesenteries (III.) has appeared on each side of the median axis, situated in the exocœle between

the dorsal directives and the dorsal pair of second cycle mesenteries. Such an early stage is to be expected on the dorso-ven-

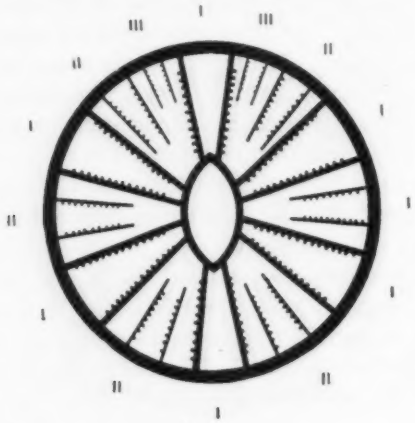

FIG. 8*a*.

FIG. 8 (*a*–*d*). Series of diagrammatic figures illustrating the order of development of the twelve pairs of third cycle mesenteries.

tral succession already established in the case of the second cycle mesenteries (p. 70).

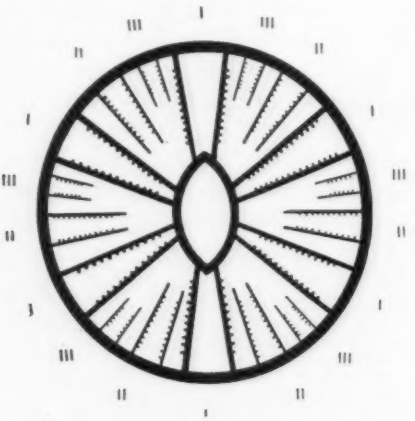

FIG. 8*b*.

The succeeding exocœlic chamber on each side lies between the dorsal pair of second cycle mesenteries and the dorso-lateral

pair of first cycle mesenteries, and it might be supposed that the new mesenteries would occupy the exocœles in regular succession from one aspect of the polyp to the other. Instead of this

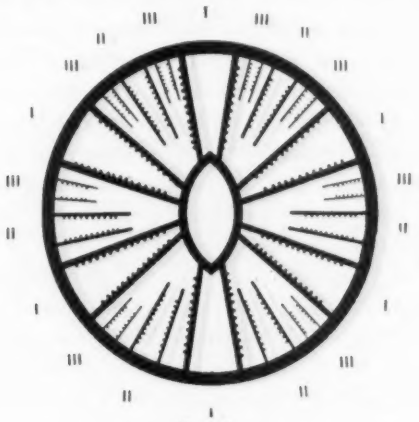

FIG. 8*c*.

the pairs are found to arise successively within only the dorsal member of the two exocœles of each system. This is shown

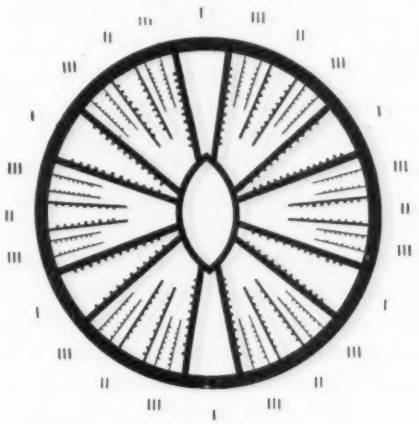

FIG. 8*d*.

in the next stage available, Fig. 8*b*, where a third cycle pair is found within the dorsal exocœle of each sextant.

A further stage secured in the growth of the twelve pairs of third cycle mesenteries is given in Fig. 8*c*, where a pair has appeared on each side within the ventral exocœle of the dorsal sextant. Clearly, if the succession thus indicated were followed with perfect regularity, other pairs would appear within the ventral exocœles of both the middle and the ventral sextants, and the cycle would then be completed according to Fig. 8*d*. No stage exactly corresponding with Fig. 8*d*, however, has been obtained, as the polyps of *S. radians* very rarely, if ever, complete the third cycle of mesenteries. Still the sequence so far as it can be traced is such as to warrant the conclusion.

The regularity in the dorso-ventral sequence of the mesenteries shown in Fig. 8 was secured only after an examination of a number of polyps. In a colony in which the polyps are so closely arranged as in *S. radians* the individuals are rarely found to undergo their later development with perfect regularity all round; some regions will be in advance of the normal sequence and others behind. The polygonal form assumed by the adults is evidence that a certain pressure is exerted upon a form which would otherwise be circular, as in the simple polyps reared from larvæ. Spatial difficulties may therefore be held sufficient to account for the irregularities appearing in the growth of the third mesenterial cycle. In *Astrangia solitaria* and *Phyllangia Americana*, where the polyps are practically free from one another, and retain their cylindrical form throughout, the regularity of development from one border to the other is more pronounced, and I have found (1902, p. 459) the order of appearance of the mesenteries to be the same as that established for *S. radians*.

The normal sequence of the third cycle mesenteries in *Siderastrea* being now established we are justified in assuming that a like succession will be maintained by the third cycle septa, as individually the septa arise shortly after the mesenteries with which they are associated. Hence the normal sequence for the members of the first three cycles of entosepta will be that represented in Fig. 9. The six septa of the first order of entosepta (I.) appear together as a cycle; the six members of the second (II.*a*–II.*c*) follow a simple dorso-ventral succession; the twelve members of the third order (III.*a*–III.*f*) also appear in a dorso-

ventral succession, but in two series — first a series of six (III.*a*–III.*c*) within the dorsal of the two interspaces in each sextant, and then the remaining six (III.*d*–III.*f*) in a like order but within the ventral of the two interspaces. As explained below, the exosepta (X.) constituting the last outermost cycle have not the same ordinal significance as the entosepta.

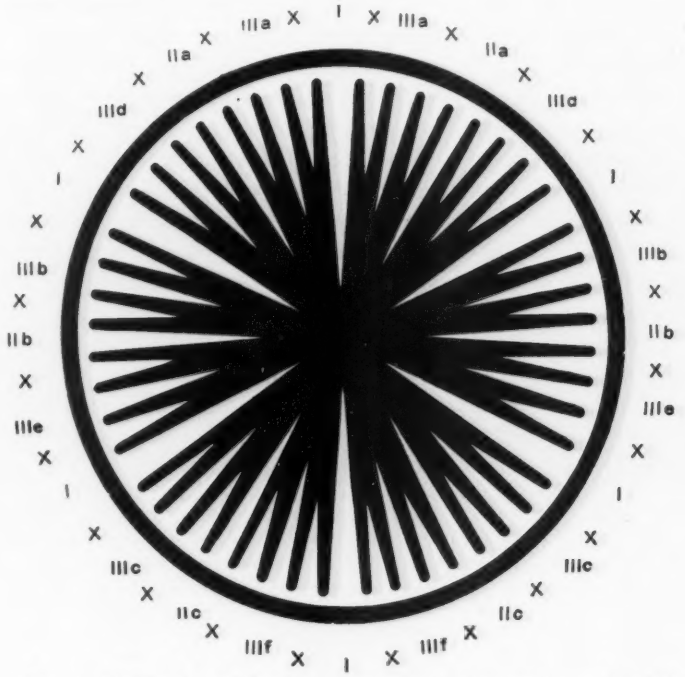

FIG. 9. Diagram showing the order of appearance of the septa in a corallite with three cycles of entosepta (I.–III.) and an outer cycle of exosepta (X.). The Roman numerals indicate the cycle to which the septa belong and the letters their sequence in the cycle.

Studies on the mesenterial sequence of other corals indicate that a similar septal succession will in all probability be followed by most forms in which the adult calice shows a regular hexameral cyclic plan. Individual departures from the order may be expected, but are to be looked upon as irregularities; regularity of growth of the higher cycles of mesenteries and septa is

by no means so pronounced as in the first and second cycles which are less likely to be influenced by spatial considerations. The sequence given is altogether different from anything which has hitherto been surmised for any coral, and further studies are desirable to determine how far it admits of general application in the group.

From what has already been revealed it is manifest that the exosepta of corals do not possess any true ordinal sequence comparable with that of the entosepta. Exosepta have been found to be present at each developmental stage, always constituting the outermost cycle, and equalling in number the sum of the inner entosepta ; but until the adult condition is reached they are merely the predecessors of the entosepta. We may consider them as the direct continuations of the primary six exosepta which bifurcate at each stage, or, less likely, as arising anew with each cycle of entosepta. Regarded as the persistent representatives of the primary exosepta they more nearly conform to the "law of substitution" in actinian tentacles as established by Lacaze-Duthiers (1872) and Faurot (1895).[1]

Studies on other corals, as well as considerations on the tentacular development in actinians, suggest that the exosepta may arise in different ways in different species of corals, and that a more

[1] In actinians generally it is found that after the protocnemic stage the tentacles appear two at a time, one entocœlic and one exocœlic, corresponding with the two chambers formed upon the appearance of a new pair of mesenteries; sometimes the entotentacles appear in advance of the exotentacles, though in *Siderastrea radians* the reverse is the case. The entotentacles when established are larger than the exotentacles, the length of the former being in accordance with the order of appearance of the cycle to which they belong, the largest being the first to appear. The exotentacles all attain an equal length and throughout are relegated to the outermost cycle, whatever be the cycle of entotentacles with which they first appeared. They constitute a single cycle of which the members are smaller than those of the cycle of entotentacles last to appear. The number of exotentacles in the last cycle is always half the total number of tentacles, the number of exocœles being equal to that of the entocœles.

Being soft polypal structures it is easy to understand how as new entotentacles are added the exotentacles become pushed aside and thus occupy different radii at different times. The septa, being hard fixed structures, do not admit of rearrangement; the new growth has to be adapted to the old, as in the fusion of the new entosepta with the old exosepta.

The tentacles, like the septa, thus arise in such a manner that it is impossible to determine their order of development from their relationships in the mature polyp.

precise significance as to their relationships at different stages may be forthcoming than is possible in *Siderastrea*. There are indications that in some forms an entoseptum and an exoseptum arise together, thus more closely recalling the method followed in the appearance of the tentacles.

The relationships now proved to exist between the entosepta and exosepta of corals involve important considerations when the cyclic hexameral sequence is not completed in the mature corallite, a condition which almost invariably happens in *S. radians*, as well as in numerous other corals. As regards both septa and mesenteries it is found in such cases that the last cycle is rarely a multiple of six, but some irregular number, resulting from the fact that at maturity the polyp does not complete the last cycle begun. Exosepta have been shown to appear always in association with entosepta, whatever be the number making up a corallite, and, as often remarked, the two series are equal in number and the exosepta outermost in position. Hence it follows that in the cyclic incompletion of the mature corallites of *Siderastrea* the third entocœlic cycle and fourth exocœlic cycle of septa vary in the same degree; whatever number of entosepta be lacking to form the complete third cycle of twelve a like number will be wanting from the twenty-four exosepta which should form the fourth cycle.

When describing the number of septal cycles within a calice of which the cyclic hexameral plan is incomplete it is usual in systematic works on corals to regard the hexameral multiples as completed so far as the number of septa will permit, and then to relegate to the last cycle all the surplus septa not included in the hexameral formula. The cycles are all supposed to be hexamerously complete with the exception of the last. Thus, with regard to *S. radians*, Milne-Edwards states: "Three cycles of septa complete, and, in general, a variable number of a fourth cycle"; likewise Verrill (1901, p. 133), describing the same species, says: "They [the septa] form three complete cycles, with part of the fourth cycle developed, so that the number is usually 36 to 40."

The relationships now established between the entosepta and

exosepta indicate that the above formulæ do not express the true morphological character of the septa. Any hexameral incompletion in the number of septa making up a corallite affects both the entosepta and the exosepta, that is, both the penultimate and the last cycles; if any septa be wanting to complete the hexameral multiple of the last cycle of entosepta the same number will be wanting from the outermost cycle made up of exosepta. The third complete cycle as understood by Milne-Edwards and by Verrill is really made up of both tertiary entosepta and of tertiary exosepta. The two kinds of septa are obviously of very different value in their development and relations to the mesenteries, and, as a matter of fact, will scarcely be of the same thickness and radial length to justify their being regarded as members of one cycle.

The cyclic formula, as usually understood in systematic works, may be written, 6, 6, 12, X, where X will represent any number from one to twenty-four. Formulated in this way the number 12 conveys the impression that the third cycle is really completed, that all the remaining septa belong to the next or fourth cycle, and that it alone is numerically incomplete. But beyond the two first cycles the septa of the penultimate and last cycles are formed concurrently, or almost so, in pairs, and incomplete cyclic hexamerism, as met with in *S. radians*, is really an intermediate condition in the establishment of two adult hexameral cycles, not of one alone, and attention should be drawn to this in the septal formula.

According to the relationships above established the morphological septal formula for *S. radians* should be written 6, 6, X, $6 + 6 + X$. In this formula the numbers 6, 6, represent the septa in the first and second completed entocycles, and X the number in the third entoseptal or penultimate cycle which does not yet complete the hexameral sequence; while $6 + 6 + X$ will represent the total number of exosepta, X being the same number as before. In the calice some of the exosepta will be tertiaries and some will be quaternaries, the number of the latter being always double the number of tertiary entosepta. The formula for a corallite having 36 septa would, according to the ordinary cyclic formula, be written, 6, 6, 12, 12, whereas, con-

sidered as entosepta and exosepta, the formula would be 6, 6, 6, 18; the three first numerals in the latter indicate the entosepta and the last the exosepta. The cyclic formula of a corallite with 40 septa would be 6, 6, 12, 16, and the morphological formula 6, 6, 8, 20. In the first morphological formula 12 of the exosepta will be quaternaries and 6 will be tertiaries; in the second 16 will be quaternaries and 4 tertiaries.

Where the relationships of the septa to the mesenteries are clearly known the morphological formula will more nearly express the real value of the septa than the ordinary cyclic formula, the latter has little significance unless the hexameral sequence is fully completed. One is not justified in saying that a cycle is really complete unless all its constituents have the same morphological value, and this is not the case when some are entosepta and some are exosepta.

A few remarks may here be made concerning the dorso-ventral appearance of the organs in corals generally, and the consequent marked bilaterally of the calice for the time being.

In palæontological literature much has been made of the fact that the Palæozoic rugose corals (*Tetracoralla*) are bilaterally symmetrical, while most modern corals are radially symmetrical. The results here outlined prove however that modern corals are strongly bilateral in the course of their development, and that it is only when the septa are fully established that an approximate radiality is assumed. In like manner I have found that many rugose corals attain perfect or almost perfect radiality when maturity is reached, though the developmental stages are strongly bilateral. Radiality in the *Actinozoa*, as compared with bilaterality, seems to have a more ontogenetic than phylogenetic significance. Furthermore, beyond the six primary members the septa in the *Rugosa* are added in a manner altogether different from that in modern hexameral corals, hence the bilaterality of the one group has a different origin from that of the other. The subject of bilaterality in the *Rugosa* will be more fully discussed in a later paper.

In modern corals the bilaterality of the polyp during development may be looked upon as associated in turn with each cycle

individually. Any cycle of septa or mesenteries tends to attain its radial condition before the next cycle commences to form, when the additions take place in such a manner as to again confer bilaterality upon the polyp as a whole. Thus the first two cycles of septa become truly radial before an additional cycle commences, when the growth of this is continued in a bilateral manner; likewise the new second and third cycles assume their radial stage before the members of the fourth cycle made their appearance, these also proceeding from one border to the other. In like manner the first cycle mesenteries are nearly radial before those of the second cycle arise and introduce a conspicuous bilateral symmetry; on the second cycle mesenteries assuming the radial plan the third cycle members begin to appear, again in a bilateral manner.

The successive dorso-ventral growth followed by the constituent mesenteries and septa of each cycle also confers a certain individuality upon the cycle. The different cycles, arising independently, seem to represent so many distinct recurring phases of growth in the life of the polyp; they do not constitute a continuous addition from one border to the other, as is usual in permanently bilateral animals, particularly segmented forms. The members of a cycle appear in a dorso-ventral sequence and may retain their differences in size for a long time, but in the end they become equal and thereby confer radial symmetry upon the polyp. Then another cycle commences to form in somewhat the same bilateral dorso-ventral succession, displays for a time the consecutive origin of its members, and afterwards attains radiality.

The conception of recurring phases of growth in cyclic coral polyps is best realized when comparison is made with the mesenterial increase characteristic of the Ceriantheæ and Zoantheæ. In the former the mesenteries beyond the protocnemes always develop in a regular bilateral successive manner, from the dorsal (anterior, sulcar) to the ventral (posterior, asulcar) aspect, the oldest being dorsal or anterior and the youngest ventral or posterior, recalling more the method followed by segmented animals; there is in the Ceriantheæ never a reversal of growth to the anterior end, followed by a successive series to the other, such as occurs in ordinary hexactinians. Employing the term "band of

proliferation," introduced by van Beneden in 1897, we may say there is only one median band of proliferation in cerianthids, while in hexactinians there are many such bands occurring all round the polyp, the number increasing with age — at first six, then twelve, twenty-four, etc.

In the Zoantheæ also mesenterial development is always in the same succession after the protocnemic stage. The increase takes place within only two of the six primary exocœlic chambers, one on each side of the ventral directives; there are only two bands of proliferation or zones of growth. In this case, however, the order followed by the new mesenteries differs from that in hexactinians and cerianthids; it proceeds from the ventral (posterior, sulcar) to the dorsal (anterior, asulcar) aspect of the polyp, not from the dorsal to the ventral.

The bilateral development of the organs, from one border of the polyp to the other, in ordinary actinians and corals would seem to have no phylogenetic significance beyond the group of the cœlenterates; indeed, even here we appear to have as yet no definite understanding as to what its meaning may be. The approximate radial symmetry of adult cœlenterates is assumed from very diverse developmental conditions (*cf.*, hexactinians, zoanthids, cerianthids, and the tentacles and other cyclic organs in the Hydromedusæ and Scyphomedusæ). Whatever may be said in favor of the well-known view that the mesenterial arrangement in cerianthids suggests the metamerism of higher animals there is clearly no support for such a conception in the development of the organs in hexactinians. In this latter group we are concerned with a radial cyclic repetition of the organs, even though the members of each cyclic series arise in bilateral succession from one border to the other.

Summary.

1. In the coral *Siderastrea radians* the six members of the first cycle of septa appear simultaneously, shortly after fixation of the larva, situated within the entocœles of the first cycle of mesenteries.

2. Six members of a second cycle are developed within the primary exocœles shortly after the primary cycle of septa. They are the temporary predecessors of a later permanent cycle,

and arise either simultaneously or in bilateral pairs in a dorso-ventral order. Later, they become bifurcated peripherally, either by the direct extension of the original septum or by the production of separate fragments which subsequently fuse. The bifurcations also appear in a bilateral dorso-ventral order.

3. The six members of the permanent second cycle of entosepta arise within the entocœles of the second cycle mesenteries soon after these make their appearance. The two right and left dorsal septa appear first, then the two middle members, and, at a much later period, the two ventral, the series thus exhibiting a decided dorso-ventrality. In the end they become equal, and each fuses with the central part of the corresponding second cycle exoseptum previously developed, these exosepta thereby losing their individuality.

4. Twelve members of a temporary third cycle are situated within the exocœles between the primary and secondary pairs of mesenteries, and represent the bifurcated extensions of the six primary exosepta. The original second cycle exosepta thus become the third exocœlic cycle, their place having been taken by the new second cycle of entosepta.

5. A new third cycle of twelve (or less) septa arises on the appearance of the pairs of third cycle mesenteries, in a similar manner to that followed by the second permanent cycle. New entosepta appear within the entocœles of the third cycle mesenteries, and the bifurcations of the third cycle exosepta then become the exosepta of the fourth cycle.

6. The third cycle entosepta, following the mesenteries, are developed in a bilateral dorso-ventral order, but in two series; first a series within the dorsal moiety of each sextant, and then a second series within the ventral part of each sextant.

7. Exosepta are present at each cyclic stage in the growth of the corallum, alternating in position and corresponding in number with the sum of the entosepta. They never become entosepta, but always constitute the outermost cycle of shorter septa; only the entosepta have any ordinal significance. Until the adult condition is reached the exosepta are the temporary predecessors of the entosepta. The developmental relationships between the entosepta and exosepta are closely comparable with

those between the entotentacles and exotentacles. The law of substitution, first discovered by Lacaze-Duthiers for the tentacles of Hexactiniæ, is thus found to hold also for the septa.

8. Where the cyclic hexamerism of a corallite is incomplete the ordinary cyclic formula does not express the true relationships of the septa; the entosepta and exosepta vary in the same degree, so that the true morphological septal formula for a corallite with three cycles and part of another is 6, 6, X, $6 + 6 + X$, where X may be any number from 1 to 12.

9. The cycles of septa and mesenteries represent so many distinct recurring phases of growth at intervals all round the polyp, not a continuous increase from one extremity to the other as in metameric animals. With the exception of the first the members of each cycle follow a dorso-ventral succession, display a bilateral symmetry for some time, and ultimately assume an approximate radial plan. The succession for the third cycle of entosepta is two-fold.

REFERENCES.

Delage, Y., and Hérouard, E.
'01 Les Cœlentérés. Traité de Zoölogie Concrète, tom. II., Pt. 2. Paris.

Duerden, J. E.
'02 West Indian Madreporarian Polyps. Mem. Nat. Acad. Sciences, vol. VIII., 7th Mem.

Faurot, L.
'95 Études sur l'anatomie, l'histologie et le développement des Actinies. Arch. de Zoöl. Exp. et Gen., ser. 3, vol. III.

Gardiner, J. S.
'02 South African Corals of the Genus Flabellum, with an account of their Anatomy and Development. Marine Investigations in South Africa. Vol. II., Cape Town.

von Koch, G.
'81 Mittheilungen über das Kalkskelet der Madreporaria. 1. Das Vermehrungsgesetz der Septen. Morphl. Jahrb., bd. VIII.

von Koch, G.
'82 Ueber die Entwickelung des Kalkskeletes von Astroides calycularis und dessen morphologischer Bedeutung. Mitt. a. d. Zoöl. Stat. zu Neapel, bd. III.

von Koch, G.
'97 Entwickelung von Caryophyllia cyathus. Mitt. a. d. Zoöl. Stat. zu Neapel, bd. XII.

Lacaze-Duthiers, H. de.

'73 Développement des Corallisires. Deux. Mém. Actiniaires à Polypier. Arch. de Zoöl. Exp. et Gén., tom. II.

Lacaze-Duthiers, H. de.

'94 Faune du Golfe du Lion. Evolution du Polypier du Flabellum anthophyllum. Arch. de Zoöl. Exp. et Gén., 3 ser., tom. II.

Lacaze-Duthiers, H. de.

'97 Faune du Golfe du Lion. Coralliaires. Zoanthaires Sclérodermés. Arch. de Zoöl. Exp. et Gén., 3 ser., tom. V.

Milne-Edwards, H., and Haime, J.

'57 Histoire Naturelle des Coralliaires ou Polypes proprement dits. Paris, 1857–60.

Schneider, A.

'71 On the Structure of the Actiniæ and Corals. (Translated by W. S. Dallas from the Sitzungsbericht der Oberhessischen Gesselschaft für Natur- und Heilkunde, March 8, 1871) Ann. Mag. Nat. Hist., 4 ser., vol. VII.

Semper, C.

'72 Ueber Generationswechsel bei Steinkorallen und über das M. Edwards'sche Wachsthumsgesetz der Polypen. Zeit. f. Wiss. zoöl., bd. XXII.

Verrill, A. E.

'01 Variations and Nomenclature of Bermudian, West Indian and Brazilian Reef Corals, with notes on various Indo-Pacific Corals. Trans. Conn. Acad. Science, vol. XI.

EVOLUTION IN A DETERMINATE LINE AS ILLUSTRATED BY THE EGG-CASES OF CHIMÆROID FISHES.

BASHFORD DEAN.

Recent attempts to explain evolutional processes, whether, *e. g.*, by natural selection, orthogenesis or use-inheritance, have been based, with but few exceptions, upon parent and offspring, in the direct relation of one to the other. Thus, (1) in the newly developed field of biometrics, variations in parent and offspring, have been discussed in terms of precision; (2) in embryology and embryopathology, ingenious experiments have tested the latent possibilities of the offspring at different stages in its career, and (3) on the side of paleontology, variations of progeny and parents have been examined on a giant scale in terms of survival and obliteration of masses of individuals. On the other hand observations are scanty, even in the present outburst of literature, which test the relation of the young to its parents by *indirect* means. This is, none the less, a line of inquiry which bids fair to become a fruitful one. And we may even at the present time consider what materials can be obtained which shall provide a series of parallel changes between the offspring and, *e. g.*, *some other product* of the parent, and through such means furnish, as it were, a *point d'appui* for evolutional studies. Thus: Are there any means of ascertaining whether an animal in providing for its progeny can produce structures *which form no organic part of the young yet which at the same time indicate accurately what the young will need in the distant future. And if these structures do occur, are they sometimes so special in their nature that they cannot be interpreted as general provision for the embryo, but rather for the late and complicated needs both of the genus for which they are provided and even of the species?* Obviously the parent has physical continuity with its young, but has it more than this? Has it the power to anticipate accurately the needs of the young, which it abandons and with whose subsequent fate it

clearly has nothing to do? Can it, for example, start an egg on its course of development and then provide it with a capsule whose special structures shall "foresee" accurately what the young is to become? Can it form a capsule which shall have the power, in spite of its lifeless substance, to develop as the enclosed egg develops, so that at each period it can best serve the corresponding stage of the embryo's growth? Such instances, if they can be found, are evidently of value in the examination of the complex problems of heredity.

The following notes are given since they appear to illustrate an extreme case in point: and since they also indicate that somewhat similar "purposeful" conditions may be demonstrated in the secondary embryonic membranes of other forms, *i. e.*, that these structures may be found the better adapted to the *future* grade of development of an embryo than has hitherto been suggested.

In examining the shark-like fish, *Chimæra* (*C. colliei*), the egg-capsule was found to be specialized, *i. e.*, adapted for the embryo at a late stage of development, rather than for the egg, in the following characters (Cf. figures in BIOL. BULLETIN, 1903, Vol. IV., pp. 271, 272):

I. *In Size.* — The capsule is not fitted to the egg; in fact, the outline of the egg is squeezed into a long ellipse, in order that it may be contained in the case, for if the case be opened and the tension relaxed the egg regains its circular outline, and the capsule with its appendage is then much (about nine times) longer than the egg. The great size of the capsule (longer in proportion to the adult body than that of a single egg of any known animal) is in evident adjustment to the advanced development of the young fish at the time it is cast upon its own resources. In point of fact it is then well grown — about one fifth the length of the adult — and by this time it has entirely lost its yolk and resembles the parent in remarkable detail — in axial and appendicular skeleton, in fins, viscera, in dermal, even in secondary sexual characters, *e. g.*, clasping organs of male.

II. *In Shape.* — The capsule as laid down in the oviduct is divided into special regions destined to contain the snout, trunk and tail of the young (at time of hatching). In earlier stages

the egg was contained in but a single region (trunk region) of the capsule. In a word, the capsule is destined to fit the shape of the embryo when full grown as accurately, to seek for a comparison, as the mummy case its mummy.

III. *In Permanence.* — The development of the young *Chimæra* is slow, taking many months, perhaps a year in hatching. The capsule is adapted to future conditions in its shape and texture, enabling it to resist wear and tear as well as the softening action of the water. Its "life," in other words, corresponds with the duration of the embryo's period of incubation.

IV. *In Attachment.* — During its long service the capsule is insured against displacement and attendant injury by means of specialized structures. These include a definite stalk, long, tough, springy, and a disc- or bulb-shaped terminal, capable of durable attachment.

V. *In Position.* — Experiments with capsules containing eggs show that when there is even a slight movement of water the capsules, as they lie on the bottom, assume a position with the keel side upward. This is the side which is dorsal in the orientation of the embryo and which bears the lid through which the fish later escapes. Furthermore, the capsule is provided with a vertical and a pair of lateral expansions which, if a current of water is present, cause it to rotate like a weather-vane in the direction of the oncoming stream. By this means the young fish is adjusted to its respiratory current and at the same time protected against the injuries which would follow the continual dislodgment of the capsule.

VI. *In its Orientation with Respect to the Growing Embryo.*—The germinal disc and early blastoderm in about fifty capsules examined occupied a constant position with reference to the capsule, appearing on the keeled side, and when the young embryo could be determined the head always pointed in the direction of the large end, *i. e.*, the operculate end, of the case. The same position is maintained in later stages, the head directed toward the large end of the capsule, the tail gradually invading the narrow sheath-like end. Symmetry is maintained with reference to the sagittal plane of the capsule.

VII. *In its Arrangement Enabling the Imprisoned Embryo to*

Obtain a Circulation of Water. — This the capsule provides by means of an elaborate system of perforations. These are bilaterally arranged, one series situated directly above the future gill region of the embryo, and a second series in the sheath in which the tail develops. These rows of perforations, moreover, are graduated in size, suggesting that in certain regions the perforations are adapted to functional needs. The embryo causes a water current to enter above the gills and to pass out on either side of the tail. (Cf. the turning of the capsule against the current, like a weather-vane.) In this connection the writer notes that he has seen the embryo execute vigorously a rhythmic undulating movement of its greatly elongated tail, which, provided with a continuous dorsal-caudal and anal-caudal fin, can only be interpreted as a specialized organ for forcing the water backward through the case.

VIII. *In its Elaborate Provision for the Escape of the Embryo at Term.* — By a delicate adjustment of the folded dorsal wall of the capsule, a line of separation is formed in the respiratory perforations above the gill-region. Thus arises an opercular flap, which finally opens in a way which suggests the opening of the lamellar beak of a duck, and thus enables the young fish to escape. This arrangement is a remarkably complicated one, the valve being provided, among other things, with roll-over margins which preclude its being opened from without and so perfectly adjusted that it opens only to the necessary degree. Once opened, moreover, the valve margins cannot be restored in their former relations, thus indicating that a state of tension has existed, comparable somewhat to that of dehiscent seed capsules.

IX. *In the Progressive Changes in the Lifeless Substance of the Capsule which take place pari passu with the Developing Needs for these Changes on the Part of the Growing Embryo.* — At the time the capsule is deposited it admits no water to its interior. In fact, the unused tail sheath is then entirely filled with a plug of thick albumen. The perforations are formed by a process of weathering, during which delicate septa obstructing the openings are gradually broken down and thus a greater current of water is admitted to the interior of the capsule. In later stages these openings are largest and most numerous. By the same process

the opercular flap, *i. e.*, the opening valve, is prepared progressively, so that the embryo can escape in due time.

X. *In its Provision for the Latest Embryonic Characters in Different Species.* — The egg capsules of four species of *Chimæra* known to the writer, present distinctive characters, and among these are some which are prophetic of the structures of the adult fish. Thus the tail sheath of the capsule of *C. colliei* is thick and relatively short, fitting the tail of the embryo of a species in which no adult opisthure is noticeable: in *C. mitsukurii*, on the other hand, the opisthure of the adult is of extreme length, and the tail sheath of its egg capsule is correspondingly long and delicate. The egg cases of *C. phantasma* and *C. monstrosa* suggest correctly intermediate conditions in the adult opisthures.

To return to the theme of the present paper: A point of general interest presented by this complicated capsule is its bearing upon the factors of evolution. For, considering always that the substance of the capsule is only indirectly connected with the egg, *i. e.*, as a secretion formed by the parent after the mechanism of heredity has already been established in the egg, it nevertheless (1) "foresees" with startling exactness the size and shape of the young fish when many months hence it comes to hatch out, and (2) it provides a series of progressive modifications adapted to the developing physiological needs of the young. It is evident, accordingly, that if natural selection be adduced to explain the present phenomenon it encounters difficulties more numerous and complex than in usual instances. In the latter cases selection concerns itself with variations which affect the progeny directly; but in the present case variations must have occurred in the lines *both* of the progeny and, indirectly, of its far less individual capsule-forming capabilities — with the result that a succession of closely correlated steps in variation must have coincided in both distinct directions.

To make more apparent the complicated nature of this procedure an example might be devised in which numbers appear. Thus: At each point in the development of the young *Chimæra* let the number of important fortuitous variations be represented by 1,000 (which I think all will agree is a number of possibilities

modest rather than excessive). And let the same number of possible variations be present in each of the various stages in the development of the capsule. Accordingly, at the first stage let us grant that variation number 673 happened to be the most favorable one: this then was selected in both the embryo and in the capsular secretion; at the second step some number, *e. g.*, 973 was similarly selected in both; at the third, number 14 in both; at the fourth, number 467 in both; at the fifth, number 801 in both; and at the two hundredth, number 761 in both. In other words, if we reckon the progressive series as extending over but two hundred steps, taking this number merely for the sake of example, as the possibilities are multitude, the chances are obviously remote of establishing the foregoing coincidences in the two series (one representing the development of the egg, the other of the capsule) by constantly repeated selection of fortuitous and fluctuating variations. For, taking the first coincidence of a favorable fortuitous variation of the embryo selected by a favorable fortuitous variation in the capsule, or indeed, even a coincidence of variations which are passable, not optimum, in both, it is evident that we are dealing with an accident of an improbable character. Thus, for variation 673 of the embryo to have seized upon variation 673 of the capsule there is but one chance in a thousand. Granted, however, that this unexpected result happened: for the second optimum variations in egg and capsule to have coincided, say the number 973 in both, there is again but one chance in a thousand, — or in other words, the chance for coincidence in the favorable selection of the optimum fortuitous variations one and two, the chances would be one in a million; of variations one, two and three, one in a billion.

It would be urged, on the other hand, by selectionists that these figures are misleading, since with hosts of variations taking place in each stage of egg and capsule there would always be a coincidence of one favorable (although perhaps not the best) variation in the egg with a correspondingly favorable (perhaps not the best) character in the capsule. But this assumption leads to no essential change in the result, for in this case if the variations do not correspond with fair accuracy, at successive stages the embryo will not fit the conditions of the capsule, and

must accordingly perish.[1] In other words, in the first stage of variation, assuming again variations 1 to 1,000 in egg and in capsule, the chances for coincidence of even passable variations would be so small that a vast proportion of the embryos would fail to mature. And of the small number which did survive the first selection the majority would evidently be eliminated in the second stage of selection. For one egg, in short, to have run the gauntlet of the favorable variations in the capsule there must have been, and must still be an enormous proportion of failures.[2] The latter is evidently false, for it was found that the eggs of *Chimæra* are about as hardy and fruitful as the eggs of other sharklike fishes. Morever, if it is necessary to show still further the insufficiency of this selectionist argument, one need only reflect that nature would have to support millions of adult *Chimæra* in order that there might be laid one golden egg! The race, in short, could at the best have existed but a few generations in view of its slowness of breeding and the small number of eggs (possibly a dozen a year) laid by each female. But this inference is palpably false, for we know that the race of chimæroids has been producing specialized egg capsules from Jurassic times.

Natural selection of fortuitous variations is, accordingly, clearly valueless in explaining the evolution of the present capsule. Use and disuse also are to be eliminated as factors in its development. If a neo-Lamarckian suggests that the capsule is a result of use, having been primitively moulded *in utero* around the *full grown* young, one need only reply that such a suggestion is in itself anti-Lamarckian, for why would a capsule, let alone a complicated one, be formed at all when the embryo is so fully grown that it cannot need it, and why should elaborate provision for aquatic breathing be present in a uterine capsule? One need hardly offer

[1] Thus, the proper variation for the opercular lid can only follow the favorable variation for the respiratory pores in the capsule, and these again can only follow if the capsule is of a great size, definite shape, or durable structure. And, of course, as definite an order must be followed in the stages of the embryo. And finally, the accurate regulation of time between the two must coincide. Thus the breathing pores of the shell must not open too early or too late.

[2] Admitting that "favorable," rather than optimum variations could have been successfully selected. Even organic selection, it seems to me, reduces the difficulty only in unessential regards.

the objection that in uterine development the well known law is to reduce secondary membranes rather than to increase them.

The capsule of *Chimæra* must stand, I conclude, as an instance of evolution in a determinate direction. Unhappily, however, it gives no data by which the cypher of orthogenesis can be simplified.

NEW FACTS CONCERNING BOTHRIOLEPIS.

WILLIAM PATTEN.

In the following paper, I shall present a preliminary account of my observations on a large collection of *Bothriolepis* recently obtained in New Brunswick. A more complete and fully illustrated account will be presented later.

This new material shows structural features heretofore unknown, and much that one could hardly hope to see preserved in any fossils, especially in ones so old as these.

The trunk, Fig. 1, was very slender and covered with a soft skin devoid of scales or of any other markings except those mentioned below. In spite of its delicate structure it is often only moderately compressed, or distorted. In the region of the posterior dorsal, it may present a somewhat triangular cross section, resembling that of *Cephalaspis* in a corresponding region, but without any traces of a lateral fold or of fringing processes.

A few small irregular plates, with the typical sculpture of the buckler, are imbedded in the skin along the dorsal surface, immediately in front of the anterior dorsal, and numerous minute ones are scattered irregularly over the flanks in the same region.

One specimen shows indications of a lateral groove, and, dorsal to it, a few oblong folds suggestive of segmentation.

The anterior dorsal fin is low and elongated, the posterior one very high and rounded. Both fins are often preserved with wonderful clearness, but show no other detail than a faint striation probably due to the presence of delicate subdermal rays.

The elongated tail, with its axis slightly curved, terminates in a narrow band. The dorsal margin consists of a delicate membrane, strengthened by a row of curved rods lying close together and arranged with great regularity. The basal ends of the rods are swollen, and one is turned a little to the left, and the adjacent one, to the right, of the median line. The rods extend on to the ventral margin of the terminal band, into the ventral lobe. The latter is faintly striated like the dorsal fins. Its anterior ventral margin appears to divide, as though it were continued forward

into the lateral folds, although no such folds have been detected in the trunk region.

There are no indications whatever, in either surface views or in sections of vertebral centra or arches, and the preservation of the specimens is so perfect, that there is every reason to believe such structures, even if formed of cartilage only, were absent. Neither have we found any indications of a notochord, although one may infer from the outline of the trunk that a notochord was present. It was probably surrounded by a membranous sheath of no more consistency, if as much, than that in *Amphioxus*.

Several specimens show a remarkable membranous frill protruding from the ventral and lateral margins of the posterior opening of the buckler. It extends completely across the ventral surface like a curtain, and is entirely separate from the overlying trunk. The lateral margins vary a good deal in different specimens, but, when clearly shown, they extend backwards in long lobes, which in one specimen are clearly thrown into regular folds like those indicated in the restoration. On the sides and toward the dorsal surface, the membrane appears to be reduced to a narrow fringe projecting from the inside margins of the opening of the shield, Fig. 2.

The ventral surface of the trunk extends without interruption or attachment over the frill and for about an inch over the visceral surface of the posterior ventrals. Here there is a prominent transverse ridge and a large scar on either side, probably the places of attachment of the trunk to the shield.

A large but very thin and nearly circular scale, or plate, marked with deep-lying radiating lines and with superficial concentric ridges is attached to the ventral surface of the trunk, between it and the inner surface of the posterior ventrals. The opening to the cloaca lies just above this plate, Fig. 2.

All the sectioned specimens showed the presence inside the buckler of a peculiar core, about an inch and a half long and half an inch in diameter, Fig. 2. It varies in shape in different individuals, but in all of them it has essentially the same characters and the same location in an antero-posterior direction. But its position shifts from side to side as though it were suspended in a rather large space and free to move laterally, or in a dorso-

FIG. 2. Median section of *Bothriolepis*. *A*, anal frill ; *a.f*, anal plate ; *cl*, cloaca ; *d f*, dorsal extension of anal frill ; *e*, ethmoid ; *g*, gill lamellæ (?) ; *m*, mouth ; *md*, mandibles ; *mx*, maxillæ ; *o.m*, oral membrane ; *p*, pineal pit ; *pl*, bone-like plate ; *pr*, processes for attachment of internal structures ; *r*, rostral plate ; *s*, ridge scales.

FIG. 1. Reconstruction of *Bothriolepis* seen from the side.

ventral direction. Its anterior end lies back of the cervical suture and from there it extends backwards about two thirds the length of the post-cephalic portion of the buckler. It is readily recognized by its fine, soft matrix and the concentric black lines, each line clearly and sharply defined and separated from the adjacent ones by regular intervals. The lines are similar in color and thickness to those made by the skin when seen in section. The whole structure, while puzzling, is unquestionably produced by some organic structure, not by sedimentation within an irregular cavity, or by mud accumulated within the alimentary canal. The anterior boundaries of the black lines are ill defined, but the posterior ones often form distinct loops as though the whole structure consisted of a series of broad lamellæ wrapped around a central axis, and with free, more or less separated, posterior margins. In some cases the whole mass of lamellæ is much distorted, or they may protrude from some rupture in the walls of the crushed shield. Under these conditions they still preserve their essential characters, showing that while originally soft and flexible they had at least as much firmness as the skin of the trunk. Behind the laminated portion, the soft matrix extends in an irregular undefined and structureless mass toward the cloaca. The remaining space within the buckler may be filled with a coarser matrix similar to that in which the whole animal is imbedded.

On the dorsal side of the laminated body, there are usually scattered fibrous masses, and one or more irregular, undefined bony plates, apparently attached by vertical sheets of blackened tissue to a low median ridge on the inner surface of the anterior median dorsal. Anteriorly, this ridge deepens into a prominent hollow process directed downwards and forwards toward the thickest part of the covering on the laminated core, Fig. 2.

Several specimens have been found with the mouth parts in their natural position, held there by membranes, whose contours can be determined with considerable accuracy.

The oral region, Fig. 3, is covered by an undulating structureless membrane in which are imbedded the various oral plates. The membrane is attached to the lateral and anterior margins of the head, as far at least as the shoulder on the anterior border of the mandibles. It extends backwards, underneath the anterior

ventro-laterals, as far as the large transverse ridge on their inner surface, to which it seems to be attached. It extends across the median line without interruption except between the mandibles. It also appears to be absent between the mandibles and maxillæ, Figs. 2 and 3, *o.m.*

The mandibles are thin, concave plates of bone, continuous with the oral membrane on the sides and in front, but with free

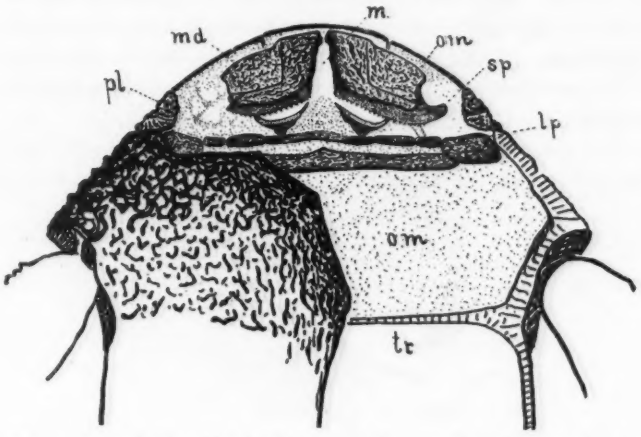

FIG. 3. Ventral side of head, with the anterior ventro-laterals removed on one side, to show extension backwards of oral membrane to the transverse ridge, *tr*; *l.p*, lateral plate attached to the two transverse bars; *m*, mouth; *md*, mandibles; *o.m*, oral membrane; *pl*, prelateral; *sp*, spur for attachment of muscles. × 1⅓.

median and posterior margins. The exposed surface presents the characteristic sculpture and the well known sensory groove. The posterior margin is nearly smooth and sharply bevelled, ending in an extremely thin edge nearly the whole length of which is broken into irregular serrations. The lateral and central serrations have more or less truncated points, the median ones are more regular in shape, sharply pointed and directed diagonally backward and inward toward the median line. The median margins of the mandibles are very thick and are provided with two horizontal edges, Fig. 4, *B*. Anteriorly the innermost edge becomes nearly vertical, forming a sharp-edged, tooth-like process, rounded in outline when seen from the side, Fig. 3. The plate

said by Woodward to unite the two mandibles does not exist. The plate seen by him was without doubt the displaced thin shelf of bone projecting backwards from the inner surface of the pre-median or ant-orbital, Fig. 2.

The notched anterior margins of the mandibles are uniformly thin and rounded, and are continuous with the oral membrane, which unites them with the margin of the head, except possibly for a short space near the median line. The lateral margin is narrow and rounded where it becomes continuous with the oral membrane. A broad spur extends laterally on the visceral side of the membrane (Fig. 3) serving no doubt for the attachment of muscles.

The visceral aspect of the mandibles is nearly smooth, except for what appear to be some indistinct muscle scars and a very

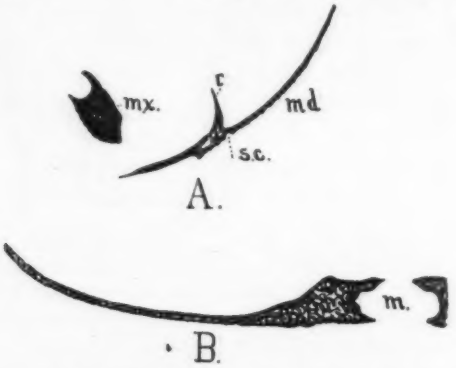

FIG. 4. *A*, sagittal section through mandibles and maxillæ, a little to one side of the median line of the head; *md*, mandibles; *mx*, maxillæ; *r*, internal muscular (?) ridge; *s.c*, sensory canal. *B*, transverse section of the mandibles to show heavy median margins. × 5½.

prominent sharp-edged ridge, which extends the whole length of the mandibles, Fig. 4, *A*, *n*.

The maxillæ are peculiar S-shaped plates lying behind, or more requently underneath, or dorsal to, the mandibles, Figs. 3 and 5. The median arm of each maxilla usually stands so as to expose a nearly smooth rounded ventral edge and a finely ornamented, somewhat triangular, strongly convex posterior surface. The median margin is undulating in outline and with a smooth border. In

sagittal sections it is seen to be deeply concave on its median posterior face, Fig. 4, *A*, *mx*.

The lateral arm of the maxilla is a narrow band, dull black and smooth. In the position shown in Fig. 3, it lies below the oral membrane with its concave surface directed upward and forward.

At the union of the two arms the band is twisted through an angle of about 45°, so that when seen directly from behind the ventral edge of the median arm forms a nearly straight line, while the lateral arm is concave on its ventral surface and on its posterior margin, Fig. 5, *A* and *B*.

The position and structure of the mandibles clearly indicates

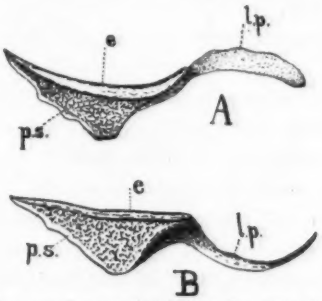

FIG. 5. *A*, maxillæ seen from ventral side and a little from behind. *B*, same seen directly from posterior surface. × 4.

that each mandible moved independently to and from the median line, so as to bring their stout crushing and cutting edges into apposition. They are frequently found with their posterior margins widely separated from the body, or even thrown forward in front of the head with their ventral surfaces facing upwards. Thus it is extremely probable that the mandibles, like two great lids or covers, could swing forwards and backwards on the membrane attached to their anterior margins, although it is improbable that they normally passed beyond the vertical position during life, Fig. 2.

The maxillæ are usually widely separate in the median line, and each was probably quite independent of the other. Their form indicates that their movements were complex. They appear to have had a rotary movement on their long (transverse)

axis, thus swinging their ventral edges forwards and backwards in a nearly horizontal plane. At the same time their median ends could be thrown forwards and medianly, thus bringing their diverging median margins more nearly parallel, and nearer together in the median line. The difference in curvature, density and rigidity between the mandibles and maxillæ, and the direction of the marginal spines on the mandibles and their absence on the maxillæ makes it very improbable that one pair acted directly against the other. It is more likely that the maxillæ merely pushed the food forward and inward, where it could be crushed, or cut, between the stout margins of the mandibles, in a manner similar to that which obtains in the mouth parts of arthropods.

I regard the paired upper and lower jaws of *Bothriolepis* as the homologues of separate right and left halves of the embryonic mandibular and maxillary arches of the higher vertebrates. As is well known these ridge-like lobes appear in all vertebrate embryos on the sides of the head, close to the nerve cord and then migrate toward the median ventral side. These embryonic mandibular and maxillary lobes I have for many years regarded as the vestiges of arthropod appendages which, owing to the special conditions under which the vertebrate head is developing, are carried toward the hæmal side of the head, instead of the neural side.

Bothriolepis is the only fish-like animal in which the halves of the jaws are separate, and functionally independent in the adult, and it thus supplies precisely the condition which the arthropod theory of the origin of vertebrates demands.

Back of the maxillæ, the oral membrane is strengthened by two bands of dermal armor. They are very thin and delicately ornamented, and when the head is in a normal position the posterior band is entirely, and the anterior one partly, overlapped by the anterior ventral plates. The narrow anterior band consists of five or six segments. The posterior one is unsegmented. Both bands are attached to a large lateral plate, the lateral end of which is bent at right angles, and attached to the lateral walls of the head, Fig. 3.

A small quadrilateral plate, that I shall call the *pre-lateral*, lies

just in front of the extra-lateral. It should be regarded as belonging to the anterior dorsal margin of the head, Fig. 1. But it is movable and is nearly always folded over on to the ventral surface, Fig. 3. It is marked with a sensory groove, probably a continuation of the anterior vertical one, although it does not appear to be exactly in line with it.

The median plate of the ocular opening is nearly perforated by a deep pineal foramen, often indicated by a low tubercle on

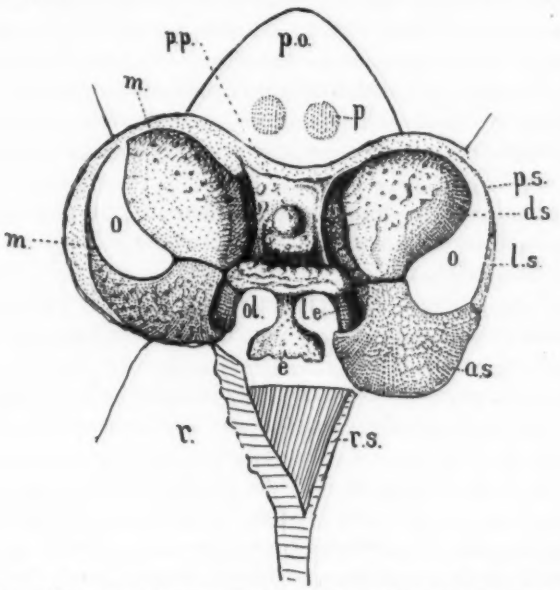

FIG. 6. Ocular and olfactory plates, in position with part of the rostral and lateral plates removed. *a.s*, anterior sclerotic; *d.s*, dorsal sclerotic; *e*, ethmoid; *l.e*, lateral arm of ethmoid; *l.s*, lateral sclerotics; *m*, membrane; *o*, corneal surface of eye; *ol*, olfactory opening; *p*, two pineal eye pits on under side of post-orbitals; *p.p*, pineal tubercle on outside of pineal plate; *p.s*, posterior sclerotics. × about 5½.

the outer surface, Fig. 6. A pair of similar pits, but not quite as deep and without any surface indications of their presence, are clearly shown on the inner surface of the small post-orbital. There is every reason to regard these three pits as similar in character and as indicating the presence of a tri-ocular median eye.

A broad thin shelf of bone extends inwards from the ant-orbital plate forming a wide chamber between the anterior surface of the T-shaped bone described by Whiteaves, or the ethmoid as I shall call it, and the two arms of the ant-orbital, Fig. 2. When the anterior face of the ethmoid is exposed, it is seen that its arms nearly enclose two circular openings, *ol*, in which the floor of the olfactory organ was probably situated, and which also served for the passage of the olfactory nerves.

These two pits clearly correspond to the antorbital fossæ of *Cephalaspis* and *Trematapis*, and thus a more satisfactory explanation of the location of the olfactory organs is furnished than the suggestion that they are situated on the margins of the mandibular plates, where there are no indications whatever of any infoldings of the oral membrane that might be regarded as olfactory organs.

Two large saucer-shaped sclerotic plates are attached by short movable arms to the lateral arms of the ethmoid, *a. s.*, and two much thinner and crescent-shaped plates, *l. s.* and *p. s.*, form the lateral and posterior walls of the orbits. The well known plate attached to the sides of the pineal plate, *ds*, completes the dorsal wall of the orbit.

All these plates are held together, and to the sides of the sensory opening, by tough but flexible membranes, leaving thus a relatively large space for the movements of the various parts. It is clear from the position of the plates in different specimens that the pineal plate could be pushed backward for several millimeters drawing the ethmoid backwards and upwards so as to open the olfactory chamber. This movement would also raise the anterior and lateral sclerotics which in turn would elevate the dorsal sclerotics and expose the eye openings, *o*, on the sides and front. The reverse movement would lower the ethmoid and draw the corneal surface of the eye into a pocket formed by the thick median margins of the adjacent cranial plates. Thus the eyes and olfactory pits could be opened and closed by the same set of movements.

The sensory canals that converge toward the median occipitals do not unite there as usually figured. Their posterior ends separate close to the median line and terminate in two small open-

ings, evidently comparable with the openings to the so called endolymphatic ducts of *Trematapis*.

In order to understand the morphology of the cephalic region of the Ostracoderms it is essential to know the location of the gills. Certain problematical structures found in the chamber in front of the ridge on the inner surface of the anterior ventro-laterals I formerly regarded as gills. I have not found any additional evidence in support of this conclusion. The presence of gills at this place would indicate that the extra-lateral was an operculum guarding the exit to the gill chamber, for it is the only cranial plate that could possibly act as such.[1] But its movements must have been very restricted and the place left for the passage of water extremely narrow, for both dorsal and ventral margins are articulated to the margins of the laterals and to the anterior ventrals respectively. The movement, such as it is, appears to be merely a tilting or partial rotation of the plate on its long axis in order to accommodate the slight dorso-ventral movement of the front part of the head, which would be impossible without some such arrangement.

On the other hand several facts indicate that the gills may have been situated in the post-cephalic portion of the buckler. These facts are (1): The presence of the superimposed lamellæ covered with what appears to be a continuation of the integument. These folds are more suggestive of gills than of any other known organs, and are almost invariably distinctly preserved, even where there is no trace of a notochord, showing that they must have had considerable power to resist decay, more, for example, than the folds in the mucous membranes of the viscera, the only other structures with which they might be compared. Moreover, if the walls of the viscera are as well preserved as this, then other internal organs should be visible in sections also, but as they are not, we are obliged to conclude that the folds in question are not produced by intestinal folds, or by any other structures of that

[1] The rather large opening in the sides of the anterior ventrals beneath the base of the pectoral spines, Fig. 1, could have hardly served any other purpose than for the passage of blood vessels and nerves to the pectoral spines.

The structure of the proximal end of the pectoral appendage indicates that some of the muscles moving the appendage were attached to the outer surface of the base of the appendage and to the outer surface of the anterior ventro-laterals.

nature. (2) The small size of the trunk at the posterior opening of the dorsal shield, and the presence of what appear to be dermal plates within the thoracic buckler, suggest that the trunk extends forwards within the buckler nearly to the head region, and that it is attached to it only along the low ridge and to the two large processes in the mid-dorsal line, to the posterior corner of the posterior ventro-laterals, where there are two large scars and a transverse ridge, and to the internal ridges near the junction of the cephalic and post-cephalic portions of the buckler. (3) The fact that the greater part of the buckler is usually filled with the same kind of matrix as that on the outside, while the part containing the finer matrix, and indicating the presence of organic material, forms a comparatively narrow band. (4) If the gills are located in this large chamber, the water must have passed out of the buckler at the posterior end, on either side of the trunk. Such a condition would harmonize with the fact that the cloaca is situated so far forward, for without such a current of water the excreta could not be easily discharged.

In conclusion, we may add that if the gills are located in the thoracic portion of the buckler, it becomes extremely probable that *Bothriolepis* possessed an atrial chamber similar to that of *Amphioxus*. The formation of such a chamber could have been brought about by the extension of the margins of the cephalic shield of such a form as *Cephalaspis* and their union on the ventral side, thus enclosing almost the whole ventral surface of the trunk from the anus nearly to the mouth, including the marginal appendages. The latter would then occupy about the same relative position as the lamellæ of *Bothriolepis*.

There has evidently been a forward extension of the ventral shield of *Bothriolepis* so as to partly cover the plates imbedded in the membrane of the oral region. The whole of this region, back to the ridge on the inner surface of the anterior ventro-laterals, with its four rows of plates, corresponds to the uncovered oral region of *Trematapis*, with its four rows of small plates surrounding the mouth.

HANOVER, N. H.,
June 21.